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SOME FACTORS IN EVERGREENNESS IN THE PUGET SOUND REGION[1]

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In this paper I propose to present some facts in regard to the extent of evergreenness in the Puget Sound region, to discuss the possible mechanisms of injury to plants by cold, and to present some data with regard to both environmental conditions and the metabolism of some plants tending to throw light on the prevalence of evergreenness in the region.

Prevalence of Evergreenness

Evergreenness is a conspicuous feature of the vegetation of the Puget Sound country. This is apparent both to the observer of the forest *en masse* and to the one who observes in detail the shrubs and even the herbs under the forest cover. There are in that portion of the state of Washington lying west of the Cascades at least 52 species of woody evergreens, 36 of which are angiosperms, and 16 gymnosperms. The gymnosperms are, of course, either such needle-leaf trees as the firs, the pines, the spruces, the hemlocks and the yew, or trees characterized wholly or partially by small scale-like green leaves, such as the cedars and the junipers.

The woody evergreen angiosperms are broad-leaf sclerophylls. The madrona (*Arbutus menziesii*) is the only member of this group that attains the size and form of a tree. The group includes, however, a large number of shrubs. Among the erect shrubs may be mentioned the rhododendron (*R. californicum*), the sticky laurel (*Ceanothus velutinus*), the manzanita (*Arctostaphylos tomentosa*), the blue huckleberry (*Vaccinium ovatum*), salal (*Gaultheria shallon*), the two species of Oregon grape (*Berberis nervosa* and *B. aquifolium*), the Labrador tea (*Ledum groenlandicum*), the swamp laurel (*Kalmia polifolia*), and among the prostrate ones may be mentioned kinnikinnick (*Arctostaphylos uva-ursi*), twin flower (*Linnaea americana*) and cranberry (*Oxycoccus oxycoccus*).

In addition to these we have some species that are deciduous under certain conditions and partly evergreen under other conditions. Cascara (*Rhamnus purshiana*) is an example of this among trees and the red huckleberry (*Vaccinium parvifolium*) is an example among shrubs. Young cascara trees growing under the forest cover retain their leaves through the winter and until the new leaves are fully expanded in May. The leaves retained through the winter do not seem to differ in appearance from those shed in the fall. The red huckleberry is mainly deciduous, but some branches bear evergreen leaves. The trailing blackberry (*Rubus ursinus*) may be mentioned as an example of a woody vine that is deciduous elsewhere, but evergreen here.

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[1] Presented at the joint meeting of the Ecological Society of America and the Western Society of Naturalists in Seattle, June 18, 1920.

Miss Pease[2] has published data on the duration of evergreen leaves in this region including the above examples. She finds that leaf duration varies widely among the different evergreen species, young cascara trees even up to ten years old, sometimes holding a part of the season's leaves until the following May, while the western yew has an extreme leaf duration of 23 years. She has also called attention to the facts about the partial evergreenness of cascara and the red huckleberry, and to the fact that a number of the broad-leaf evergreens hold their leaves only until the new ones are well grown, while some others keep them two or three years or more.

In addition to these woody evergreens we have an evergreen flora of herbaceous plants, numerous as to both species and individuals. This group of evergreens is represented by such seed plants as chick weed (*Stellaria media*), spring beauty (*Claytonia sibirica*), cat's ear (*Hypochaeris radicata*), and wild ginger. It also includes such ferns as the sword fern (*Polystichum munitum*), the licorice fern (*Polypodium vulgare*) and the deer fern (*Lomaria spicant*). There are also a considerable number of evergreen mosses and liverworts. The plants mentioned are given merely as examples of the groups, and are not to be considered as complete lists.

Structural and Physiological Factors

In the evergreen sclerophylls of the region, both needle-leaf and broad-leaf, we find the structural characters that are usually associated with evergreenness or drought, such as the absence of stomates on the dorsal surface, the grouping of stomates on certain portions of the ventral surface of the leaf and their protection by means of powdery material or hairs, the large development of cuticle, the reinforcement of the epidermis by hypodermal cells, the occasional presence of water storage tissue and the general lack of succulence. These anatomical characters, of course, have their influence on the functions of these leaves. No study has been made, so far as the writer knows, of the anatomy of evergreen herbaceous leaves.

The work of the last half century, more especially of the last decade, along the two lines of (*a*) the structure and metabolism of evergreen leaves and (*b*) the metabolic changes accompanying the hardening process in plants has made it evident that structural characters do not entirely account for evergreenness, but that the influence of the environment on the metabolism of the leaf is also a large factor. In the work that has been done along these two closely related lines of hardening and evergreenness several suggestions have been made as to the possible mechanism by which low temperatures injure the leaves of plants. More or less experimental evidence has been obtained for several of these.

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[2] Am. Jour. Bot. 4: 145–160. 1917.

The important ones may be grouped under four heads: (1) injury to the plasma membrane, (2) failure of the cell to regain the water lost by it in freezing, (3) accumulation of toxins in the cells as a result of low temperature, and (4) the precipitation of the proteins as a result of the low temperature and the metabolic changes accompanying them. The writer is indebted to Harvey[3] for the citation of the literature along these lines and has personally examined but little of it.

Some of the workers believe that injuries to the plasma membrane are important factors in the effect of freezing on plants. It is suggested that the influence may be mechanical and that the osmotic properties of the membrane are thus altered. If we think in terms of the ideas now current among many workers and regard protoplasm as a complex colloidal system of the emulsoid type and think of the difference between the plasma membrane and the interior portion of the protoplasm as being merely one of the relative water content and consequent difference in the state of dispersion of the various components of the system, then it seems evident that low temperatures may make a very great change in the physiological efficiency of this membrane, injuring the cell through turgor changes or through the loss of necessary substances. It now seems to be pretty well established that water is withdrawn from the protoplast when freezing occurs, ice being formed in the intercellular spaces. If the conditions of thawing are such that the water reenters the protoplast, the cell may be uninjured by this temporary withdrawal of water. If, however, the water withdrawn by freezing does not reenter the cell readily on thawing, serious consequences may follow merely from the absence of the water from the protoplast.

It is believed by some workers that low temperatures surrounding leaves so lower the rate of oxidation in them that toxic substances accumulate at low temperatures, which would be oxidized to non-toxic substances at ordinary temperatures. This idea is consistent with much of our knowledge of organic toxins.

The idea has been advanced that frost injury is due to the precipitation of the proteins through salting out. It is believed by several workers that the concentration of salts in freezing becomes sufficient to cause irreversible precipitation of the proteins in solution in the cell sap and to cause similar changes in the protoplasmic gels.

We come now to the consideration of how the structural characters and the various factors of the environment in this region may operate to produce such prevalence of evergreenness as we see about us in the Puget Sound country.

[3] Jour. Agr. Res. 15: 83–112. 1918.

Again the writer is indebted to Harvey,[4] whose thorough experimental work on the hardening of plants and exhaustive correlation of the literature of the effects of low temperatures on plants furnishes much that is suggestive in the problem of evergreenness in this region. He found that the first indication of frost injury to succulent plants was the freezing of local areas of the leaf. He believes that the whole leaf may be slightly under-cooled and freezing occur only when inoculation occurs from ice formed on the surface of the leaf. He finds that wax on leaves prevents this inoculation and thus prevents frost injury. An anatomical study of the evergreen herbaceous leaves of this region might throw some light on this particular phase of the evergreenness.

The extent to which under-cooling may occur before freezing begins is always a question to be considered in the influence of low temperatures on plants. It is not now believed that much under-cooling occurs in leaves since the movements of the air keep them in fairly constant motion.

The available data on the possible ways in which environmental factors may modify the metabolism of leaves in such a way as to enable them to be evergreen may be grouped under four heads: (1) The accumulation of sugar in the leaf in winter, (2) the similar accumulation of oil, (3) variation in acidity as a result of temperature changes and (4) changes in the proteins correlated with temperature changes.

Data on sugars in relation to evergreenness have been obtained by Lidforss.[5] He found that the chlorophyll-bearing cells of plants that remain green during the winter were rich in sugars and wholly or partially free from starch. Similar data had previously been obtained by other workers but they had not attempted any interpretation of the facts. Lidforss suggests that the large sugar content of these leaves is probably due to the activation of a diastatic enzyme by low temperatures and to the low rate of protein synthesis at low temperatures, which results in the accumulation of asparagin, a substance favoring the hydrolysis of starch into glucose. He believes that the transformation of starch into glucose makes the plant more resistant to cold for two reasons. The first is that this decreases the freezing point of the protoplasm, and the second is that it retards the precipitation of the proteins. The first point scarcely needs elaboration. The second is tied up with the idea that death of the plant cell from freezing is due to the precipitation of the proteins, and must stand or fall with that idea. To the writer, the data supporting this idea seem sufficient to warrant its acceptance, as the situation stands at present.

Since water is extracted from the cell in freezing, and the formation of ice takes place in the intercellular spaces, one effect of freezing is to concentrate the solution of salts in the protoplast. This may result in salting out the proteins. Lidforss records experimental evidence tending to show that the presence of a non-electrolyte such as glucose decreases the tendency to protein precipitation. He finds that thin-leaf plants withstand cold just as well as thick-leaf ones. His data and his interpretation of them constitute important pioneer work in putting evergreenness on a physiological basis. Several other workers are cited by Harvey as agreeing with Lidforss "in ascribing to sugar an important rôle in the prevention of protein precipitation owing to its protective effect for colloids."

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[4] Op. cit.

[5] Lunds Univ. Arsskr. 1907.

Unpublished data obtained by Miss Karrer in this laboratory tend to confirm the accumulation of sugar at the expense of starch during the winter. She made quantitative determinations of the sugar and of the starch in leaves as shown in the following table. The first species was selected as an example of the broad-leaf evergreen sclerophylls and the second as an example of the herbaceous evergreens.

TABLE 1. *Sugar and starch determinations on evergreen leaves*

Date	*Arbutus menziesii*			*Stellaria media.*		
	Sugar in terms of glucose	Starch in terms of glucose	Ratio of starch to glucose	Sugar in terms of glucose	Starch in terms of glucose	Ratio of starch to glucose
Jan. 28	1.0739	0.1524	.14	0.7781	0.1711	.22
Feb. 5	2.1523	0.1542	.07	0.7778	0.1165	.15
" 12	2.5360	0.3483	.13	1.0402	0.1062	.10
" 21	1.5968	0.5665	.35			
Mar. 3	1.3488	0.5831	.43	0.7506	0.1174	.15
April 5	0.9784	0.7422	.75	0.6603	0.2068	.31
May 14	0.7356	0.8110	1.10	0.3024	0.3965	1.30

In fig. 1 the writer has plotted the ratio of starch to sugar as shown in the above table. Further data on the starch and sugar content of leaves from evergreen conifers, broad-leaf evergreens and herbaceous evergreens of this region extending throughout the year are highly desirable.

Miss Tuttle[6] found that the leaves of evergreen plants in northwestern Canada are destarchified as early as October and then contain a large amount of oil. She also found that the leaves of potted *Linnaca* plants placed at 20° C. in darkness decreased rapidly in oil and fat content and increased correspondingly in starch content. Controls at lower temperatures formed no starch and their oil and fat content did not decrease. Though this increase in starch content with high temperatures, accompanied by a corresponding decrease in oils and fats always occurred in *Linnaea*, it did not occur in any case in *Picea* cuttings kept in water, or in potted *Pyrola* plants.

When *Linnaea* was again placed in low temperatures its starch disappeared and oil and fats reappeared at 2° C. to —3° C. When the temperature was as low as —15° C. to —28° C., there was no decrease in starch and the cells were mostly plasmolyzed. The observational portion of her data seem to suggest that oil formation may be an important factor in evergreenness, though her experimental evidence is positive in only one of the three species tried and is entirely negative in the other two.

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[6] Ann. Bot. 33: 201–210. 1919.

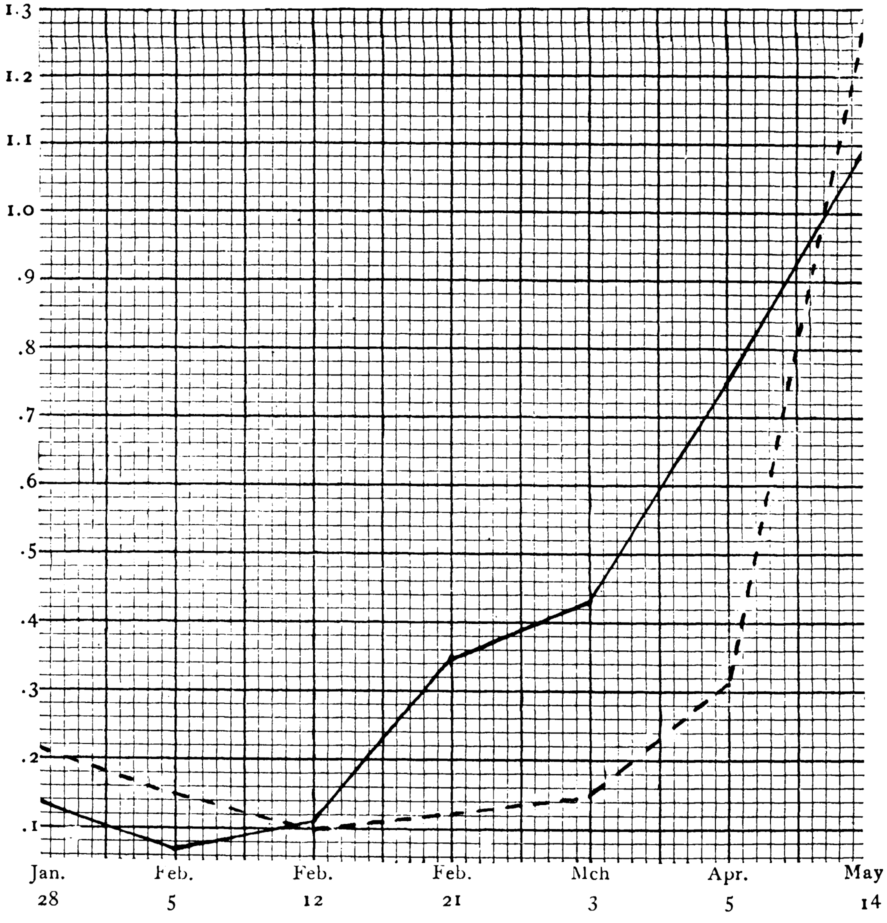

FIG. 1. Ratio of starch to sugar in winter and spring. Solid line is *Arbutus menziesii*, dotted is *Stellaria media*.

The writer knows of no work on the variation in the relative starch and oil content with seasonal changes in the Puget Sound region. Data on this would help much in the solution of the problem of evergreenness.[6a]

Harvey's work indicates that acidity is a very important factor in the effect of cold on plants. He holds that the factors causing protein precipitation when a plant juice freezes are principally the increase in the hydrogen ion concentration and the increase in the concentration of the salts. He believes that the increased salt concentration would be insufficient to account for the results observed if increased hydrogen ion concentration did not occur. He accepts the withdrawal of water and the precipitation of the proteins as large factors in the injury of plants by low temperatures. His work is, of course, concerned with the hardening process, but much of it seems to have important bearing on the factors in evergreenness. He does not believe that sugar accumulation is an important factor in the resistance of hardened plants to freezing.

[6a] Meyer believes as a result of his microchemical work on several species of evergreens that the droplets formerly supposed to be fat droplets are not fat, and that the total volume of these does not rise and fall with winter and summer, but increases with the age of the leaf. Meyer, A., "Die angeblighe Fettspeicherung immergrünner Laubblätter," Ber. Deut. Bot. Ges. 36: 5–10, 1918; Bot. Abs. 2: 96, 1919.

Harvey records also that several other workers have thought that plants hardened by exposure to moderately low temperatures withstand cold better because of changes in the nature of the proteins, one worker believing that "high molecular" forms are split to simple forms which are not so easily salted out. Harvey states that "The principal effect of the hardening process for cabbages is a change in the constituents of the protoplasm which prevents their precipitation as a result of the physical changes incident upon freezing. The proteins are changed to forms which are less easily precipitated."

Environmental Data

It is not easy to say definitely what factors in our climate may be the most important ones in the modification of the metabolism of our plants by the mechanisms suggested. There seem, however, to be some facts about our climate that are at least worth discussion from the standpoint of their influence on evergreenness.

The records of the local weather bureau which now cover a period of twenty-nine years amply support the general idea that we have a mild climate, with rainy winters and dry summers. The year 1918 may be taken as an example of air temperatures and precipitation. The maximum and minimum air temperatures by months for that year are shown in table 2.

Table 2. *Air Temperatures at Seattle for 1918*
Degrees F.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Max..	60	54	65	73	72	81	83	84	82	68	60	58
Min. .	24	26	29	34	39	45	47	48	47	39	32	27

The folowing additional data for that year may be mentioned:

Mean temperature for the year	51.6°	F.
Greatest daily range	28°	Sept. 5
Least daily range	3°	Oct. 16, Dec. 20.
Greatest monthly range	39°	April
Least monthly range	28°	Feb.
Last killing frost of spring		Mar. 7
First killing frost of fall		Nov. 27

The maximum temperature occurring in 28 years up to 1918 was 96°. This occurred June 8, 1903. The minimum for the same time was 3°, January 31, 1893. It is thus seen that temperatures in this region are moderate, extremely high or extremely low temperatures being rare.

The precipitation by months for 1918 is shown in table 3.

TABLE 3. *Precipitation in Seattle for 1918*

Inches

Jan.	2.94	Apr.	0.96	July	1.38	Oct.	3.46
Feb.	4.81	May	1.19	Aug.	1.12	Nov.	3.81
Mar.	3.92	June	0.50	Sept.	0.08	Dec.	5.04

The longest period without precipitation was 38 days and extended from August 22 to September 29. The longest period with precipitation every day was 9 days and extended from February 9 to 17. That the monthly precipitation for 1918 does not very closely approximate the average for some months is indicated by the following averages of the last 28 years. July 0.68, August 0.49, January 4.64. The greatest total precipitation for any of the 28 years was 45.78 in 1902, while the least was 21.69 in 1911. The average for the 28 years is 33.93.

These figures indicate an annual precipitation similar in total to that of the agricultural states of the upper Mississippi Valley, but distributed differently. It is in the distribution of this precipitation through the year rather than in the total amount that the Puget Sound country differs from portions of the United States lying farther east. The figures for Seattle approximate those for a large portion of the area. The rainfall of the San Juan Islands is, however, only about 20 inches per year, while along the Pacific side of the Olympic Peninsula it is over 100 inches.

Snowfall in the lower altitudes is usually very light in this region. Frequently the whole winter passes at Seattle with only one or two snowfalls, and those not enough to cover the ground. This is varied, however, by occasional winters with more snow. The extreme came in the winter of 1915–1916, when we had at Seattle a total of 154 cm. (60.9 in.). Other snowfalls worthy of note are 1896–7, 79 cm. (31.2 in.), 1898–9, 94 cm. (37 in.), and 1892–3, 147.3 cm. (58 in.).

The available data on soil temperatures at Seattle begin with June, 1918. The work on soil temperatures has been carried on by the writer under the auspices of the committee appointed jointly by the American Phytopathological Society and the Ecological Society of America to secure such data throughout the whole United States. The thermograph used is furnished by the Carnegie Institution of Washington. Table 4 gives data from July, 1918, to June, 1919.

TABLE 4. *Soil Temperatures at 6 inches. Seattle*

	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
Max.	82	82	82	66	56	47	45	43	54	61	69	74
Min.	58	60	55	47	38	32	31	31	33	39	51	54
Max. Range in any 24 hrs.	17	17	17	10	10	5	6	9	10	12	12	12

The records for the summer months show on sunny days a rather regular curve with a maximum late in the afternoon and a minimum toward morning. On cloudy days there is little variation in the soil temperature during the day. The soil in this region is rather dry during the summer months at a depth of six inches, and its temperature is very readily influenced by the sun's rays. In winter it is filled with water and is not so subject to temperature changes in response to the sun, even when the sun does shine. During this season the daily variations are slight, the record often closely approximating a straight line for nearly a whole month. The maximum soil temperature recorded is 82°, July 7, 1918 and July 15, 1919. The minimum is 31°, January 1 and 2, 1919.

DISCUSSION OF ENVIRONMENTAL DATA

The outsanding facts about the natural environment under which plants commonly live in the lowlands of the Puget Sound country are, then, as follows: (1) Moderate temperature of both soil and air throughout the year. (2) High moisture content of both soil and air in winter with low moisture content of both in summer. (3) The absence of snow.

The high moisture content and comparatively high temperature of the soil in this region in winter make the conditions for the winter growth of roots quite favorable. Cuttings of roses and other plants placed in the soil in November form root systems of considerable extent before spring. Experience indicates that in most cases early winter is the best time for transplanting in this region. This is probably explainable, at least partially, on the basis of the growth of new root tips during the winter, before the plant is put to the test of leaf or flower production under its new environment.

The high moisture content of winter certainly keeps transpiration very low. This tends to guard the leaves against such dangers as might arise from excessive loss of water from their cells during their period of dormancy.

It would seem that the conditions here are such as to produce hardening in plants.[7] They are rarely subjected to high temperatures, and during autumn and early winter they are subject to moderately low but not extreme temperatures. This must tend to harden them so that they are enabled to better withstand the occasional freezes which come during nearly every winter. Harvey found that cabbage plants exposed for 5 days to a temperature of three degrees above zero C. were then resistant to a half hour of freezing at 3 degrees below zero. Hardiness so quickly induced in these plants was, of course, quickly lost. Since sudden freezes without previous cool weather are practically unknown in this region it is possible that the leaves of certain herbaceous and deciduous plants are hardened each autumn so that they withstand the occasional extremes to which they are subjected. It is also supposable that the hardening effect may, through the course of years, be cumulative in the individual in the case of perennials or in successive generations in the case of annuals.

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[7] [It would appear as if this hardening were of a temporary nature such as to permit frost sensitive plants to withstand occasional freezing. Douglas fir (*Pseudotsuga taxifolia*) forms splendid forests in this region and yet is known to be particularly subject to injury from frost. See Pearson's "Factors controlling the distribution of forest types," Part II, ECOLOGY, Vol. I, No. 4, 1920, and Korstian's "Effect of a Late Frost upon Forest Vegetation in the Wasatch Mountains of Utah," in this issue.—ED.]

Harvey and some other workers have found that the effects of desiccation and of freezing are similar in that they both cause changes in hydrogen ion concentration and salt concentration. It would be interesting to know whether moderate desiccation and moderately low temperatures would have similar effects in enabling plants to withstand freezing, and whether the dry conditions of soil and air during Puget Sound summers may be a factor in prevailing evergreenness.

It does not seem probable that the blanket effect of snow in protecting the roots of plants from extremely low temperatures can be a factor of much importance here. The snow covering is present during few of our winters and then for a brief time only. The mechanical effect of snow in this region is occasionally seen. The writer has elsewhere[8] described the breaking down of evergreen trees by snow during the heavy snowfall of February, 1916, and pointed out that needle-leaf evergreens suffered much more than broadleaf ones. The breaking or distorting of trees by snow is, however, rare in the lower altitudes of the Puget Sound country.

In summing up the situation in regard to evergreenness in this region it may be stated that data secured locally consist of (1) the records of the local weather bureau, (2) the soil temperatures obtained by the writer with the cooperation of the Carnegie Institution of Washington, (3) the data on the duration of evergreen leaves by Miss Pease, (4) the unpublished data by Miss Karrer on the sugar and starch content of the leaves of one broadleaf evergreen and one herbaceous evergreen, and (5) the data published by the writer on snow injury to trees. With these data this paper has attempted to correlate the work done by Harvey and others on the hardening process in plants, and by Miss Tuttle on oils and fats in evergreen leaves, and by Lidforss and others on the sugar content of evergreen leaves in winter. This paper makes no pretense of presenting a completed subject; it is merely a discussion of the present state of our knowledge with the emphasis on the open questions on which further work is much to be desired.

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[8] Torreya 16: 257–260, 1916.